BREVIORA
Museum of Comparative Zoology
US ISSN 0006-9698
CAMBRIDGE, MASS. 21 FEBRUARY 1979 NUMBER 449

SOUTH AMERICAN ANOLES: THE SPECIES GROUPS. 2. THE PROBOSCIS ANOLES (*ANOLIS LAEVIS GROUP*).

ERNEST E. WILLIAMS[1]

ABSTRACT. The *Anolis laevis* group is known from three species represented by only nine specimens, all males, from four localities. All are distinguished by a soft multi-scaled proboscis and form a graded series from Peruvian *A. laevis* (proboscis minimally developed) through Brazilian *A. phyllorhinus* (proboscis of moderate size) to Ecuadorian *A. proboscis* (proboscis very long). Color in life and habitat are known only for *A. phyllorhinus*. The proboscis is interpreted as primarily an intraspecific social signal increasing the virtual size of the animals.

The most readily recognizable — at least in males — of all South American *Anolis* are the three species that have a nasal appendage or proboscis. The group may be described as follows:

Anolis laevis species group

Type species: A. laevis Cope 1876.

Definition: (Many possibly useful details are not determinable in *A. laevis* and hence are not mentioned here.) Alpha anoles of moderate size (60–97 mm snout-vent length) distinguished by a soft multi-scaled nasal appendage projecting forward *above* the rostral scale. Four to 10 scales across the snout between the second canthals. Supraorbital semicircles in contact or separated by as many as three scales. Loreal rows two to five. Interparietal of moderate to large size in contact with the surpaorbital semicircles or separated by as many as three scales. Supralabials in contact with suboculars. Middorsal scales uniform or the median row raised into a crest of triangular scales. Tail crest single or double. Lamellae

---

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

under fourth toes ranging between at least 17 and 26. Dewlap and postanals large in males. Females unknown.

Distribution: Widely disjunct: (1) trans-Andean Ecuador; (2) southern tributaries of the Amazon in central Amazonia; (3) western Amazonia.

INCLUDED SPECIES

Anolis laevis Cope 1876

(Fig. 1)

Scytomycterus laevis Cope, Jour. Acad. Nat. Sci. Phila., NS 8: 165.

Holotype. ANSP 11368, collected by Prof. James Orton.

Type locality. "Between Moyabamba and Balsa Puerto on the river Huallaga in eastern Peru."

Additional references: Boulenger, 1885: 56 (referred to the genus *Anolis* and placed between *A. tigrinus* and *A. punctatus*); Burt and Burt, 1933: 17 (listing only); Barbour, 1934; 154 (placed along with *A. tigrinus* as synonym of *A. transversalis;* both synonymies quite mistaken); Williams, 1965: 6 13 (discussed as member of the *punctatus* group *sensu lato*); Peters and Donoso-Barros, 1970. 57 (citation only); Malnate, 1971: 358 (listing of type in the Philadelphia Academy).

Anolis phyllorhinus Myers and Carvalho 1945

(Figs. 2 and 3)

Anolis phyllorhinus Myers and Carvalho, Bull. Mus. Nac. NS No. **43:** 2.

Holotype. MN (Rio de Janeiro) 1864, adult male collected by Alexandre Parko on June 14, 1943.

Type locality. "Borba, lower Rio Madeira, State of Amazonas, Brasil."

Additional references: Williams, 1965. 8-13 (discussed as member of the *punctatus* group *sensu lato,* first mention of the second known specimen MZUSP 7118, Jacareacanga, Rio Tapajoz, Pará, Brasil[1]); Peters and Donoso Barros, 1970. 63 (citation only).

Anolis proboscis Peters and Orcés 1956

(Figs. 4, 5, and 6)

Anolis proboscis Peters and Orcés, Breviora No. **62:** 2.

---

[1] Note that the region between the Madeira and Tapajoz is one of Haffer's (1974, p. 70) "distribution centers" for endemic Cis-Andean birds.

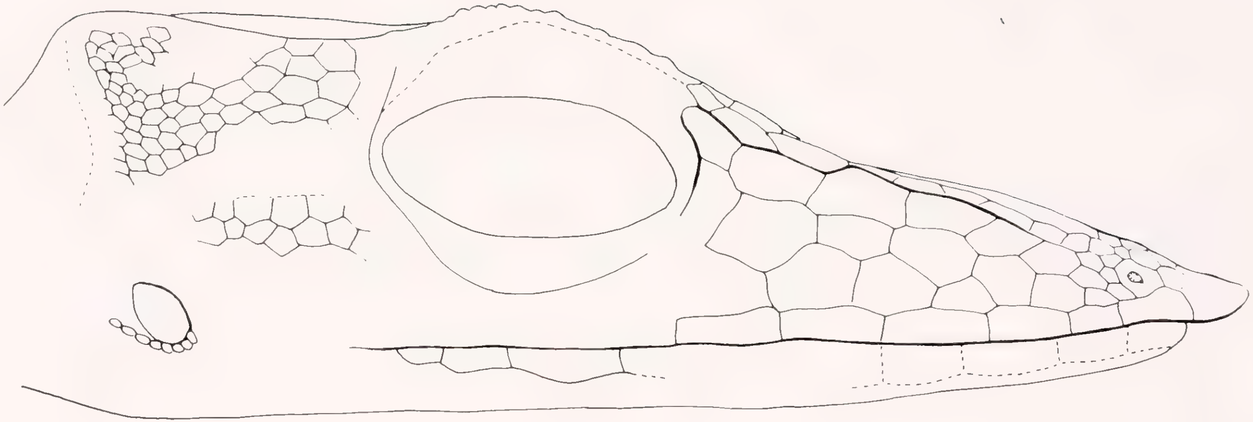

Figure 1. *Anolis laevis,* ANSP 11368. Lateral view of head of type.

Holotype. MCZ (Cambridge) 54300, a mature male collected by Antonio Proano during April 27–29, 1953.

Type locality. "Neighborhood of Cunuco, a small town at 1200 meters elevation, five kilometers northwest of Mindo, on the south bank of the Rio Mindo, a northern tributary of the upper Rio Blanco, in Pichincha Province, Ecuador." (The five additional specimens — USNM 207671–73, in the National Museum of Natural History, Washington, D.C.; IPN 7611, 7612, in the collection of Gustavo Orcés V in Quito, Ecuador — are from Mindo or "region of Mindo.")

Additional references: Williams, 1965: 8 13 (discussed as member of the *punctatus* group *sensu lato*); Peters, 1967: 13, 17 (key and citation); Peters and Donoso Barros, 1970: 63 (citation only).

Ecological information. None except for *A. phyllorhinus* Myers and Carvalho: "Mr. Parko collected the holotype of *Anolis phyllorhinus* in the capoeira (second growth or low jungle) that surrounds the town of Borba. This locality is in the Amazonian lowlands on the lower Rio Madeira, about 90 miles (airline) south-southeast of the city of Manaus. The lizard was caught on a low tree while Mr. Parko was collecting butterflies. . . ."

Distinguishing characters of the species. A. laevis differs from the two other species in the small number of scales between the second canthals (4, rather than 9 or 10), the low number of loreal rows (2, rather than 3 to 5) and in having a very rudimentary proboscis. *A. proboscis* has a crested dorsum and tail and a very long proboscis, while *A. phyllorhinus* lacks such crests and in fact has two rows of scales dorsally on the tail and a shorter proboscis. Table 1 lists the standard scale characters for each species.

Size. Snout-vent length: *laevis* 60 mm, *phyllorhinus* 73 mm, *proboscis* 74 mm. Tail: *laevis* 79 mm, *phyllorhinus* 153 mm, *proboscis* 97 mm. Hind limb length: *laevis* 39 mm, *phyllorhinus* 49 mm, *proboscis* 42 mm.

Color. Laevis: Cope reported the preserved specimen as follows: "Color above dark gray, below pigmented white (in spirits). The two colors are abruptly defined between the orbit and there are brown spots behind the axilla. Tail distinctly annulate."

Phyllorhinus — Myers and Carvalho: "Color in alcohol (formalin-fixed) plain, dull, bluish gray above, lighter beneath, with no sign of a color pattern anywhere save on the toes and undersides of the legs.

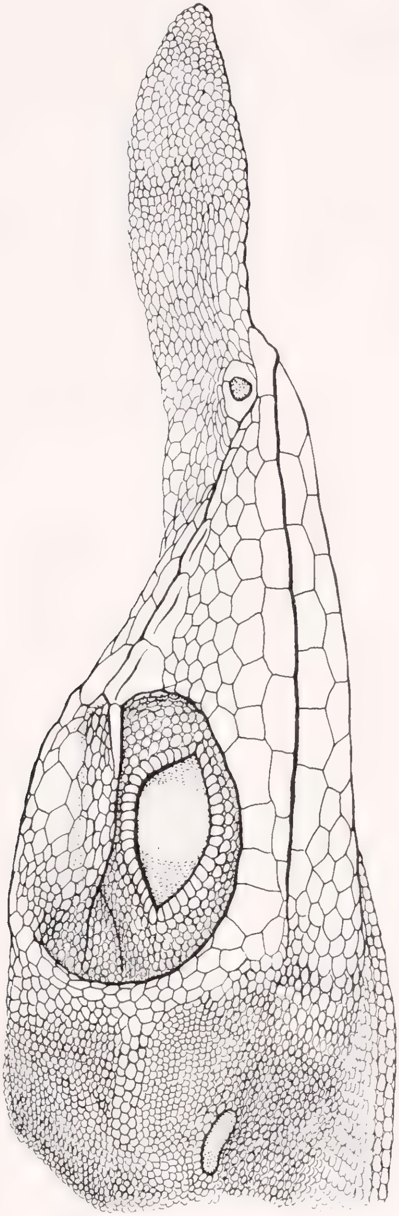

Figure 2. *Anolis phyllorhinus,* MZUSP 7118. Lateral view of head of Sáo Paulo specimen.

Table 1. Scale counts and characters.

	laevis	*phyllorhinus*	*proboscis*
	soft protuberance covered with ? small scales	leaf-like laterally compressed with granular scales	leaf-like laterally compressed with elongate scales
	N = 1	N = 2	N = 6
scales between second canthals	4 (Cope)	10	9–10
scales between semicircles	0	0	1–3
scales between interparietal and semicircles	0	1–2	1–3
loreal rows	2	4–5	3–5
rows between suboculars and supralabials	0	0	0
labials to center of eye	?	6–7	9–12
sublabials in contact with infralabials	?	5–6	2–3
median gular scales in contact with mental between sublabials	?	4	2
middorsal rows enlarged	0	0	1 (crest of triangular scales)
tail crest	double row, no crest	double row, no crest	crest present
lamellae 4th toe	?	25–26	17–21

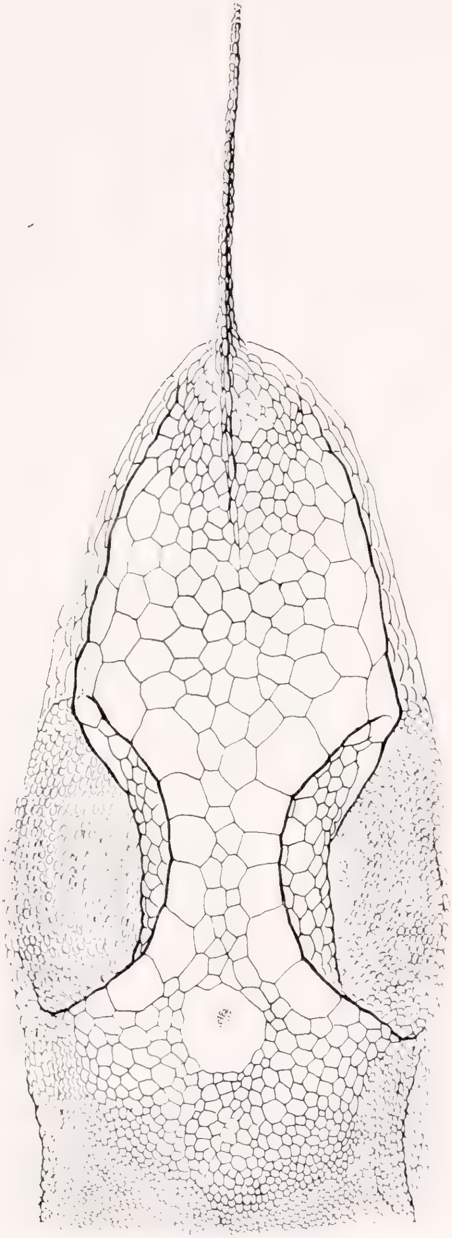

Figure 3. *Anolis phyllorhinus*, MZUSP 7118. Dorsal view of Sáo Paulo specimen.

The undersurfaces of the legs and arms bear a fine, light mottling, perhaps better described as a bluish reticulation on a yellowish ground color. The undersurfaces of the digital expansions are dark. The superior surfaces of the toes and fingers (but not of the feet and hands) are light, with bold, blackish crossbands. The tail gradually becomes brownish toward the end. A color sketch made by Mr. Parko from life shows the creature bright blue-green, the dewlap yellowish, with traces of pink or red on the toes, the top of the snout, and the end of the rostral appendage." Mr. Parko's notes say the beast immediately changed from bright blue-green to brown when captured, but changed back to green on preservation.

Proboscis — Peters and Orcés: "Dorsal ground color (in alcohol) a dull gunmetal blue, with irregular, parallel, horizontal black streaks along vertebral margin. These streaks vaguely line up and form a pair of lateral bands between the limbs. Dark brownish-black spot at shoulder. Limbs and lateral surfaces spotted with light yellowish white; limbs vaguely barred with darker blue; skin in interstices between scales of dorsum of digits light, giving appearance of banding on fingers and toes. Dorsum of head unicolor, as back; temporal region and lips lighter, with faint reddish or purplish tinge and a marked light spot over ear opening. Ventral surfaces generally lighter, with vague reddish tints on chest and chin; belly stippled with light spots. Venter of limbs heavily spotted with white proximally, becoming totally white on the foot. Tail alternately barred with gunmetal blue and blackish bands approximately equal in width."

TAXONOMY AND NOMENCLATURE

The single recognition character — the proboscis — differs considerably in the three known species, which are abundantly distinct. The extent of the differences might reasonably raise the issue of parallel evolution, but the proboscis is so singular a feature that it seems subjectively more probable that the known species are the relicts of a once much larger radiation. It is also very possible that there are more species still to be discovered, perhaps with quite restricted distributions.

It is clear that the first adumbrations of a proboscis are found in *A. punctatus* and some of its relatives. In these the rostral scale and rostral area are produced to overhang the lower jaw. In *laevis* there

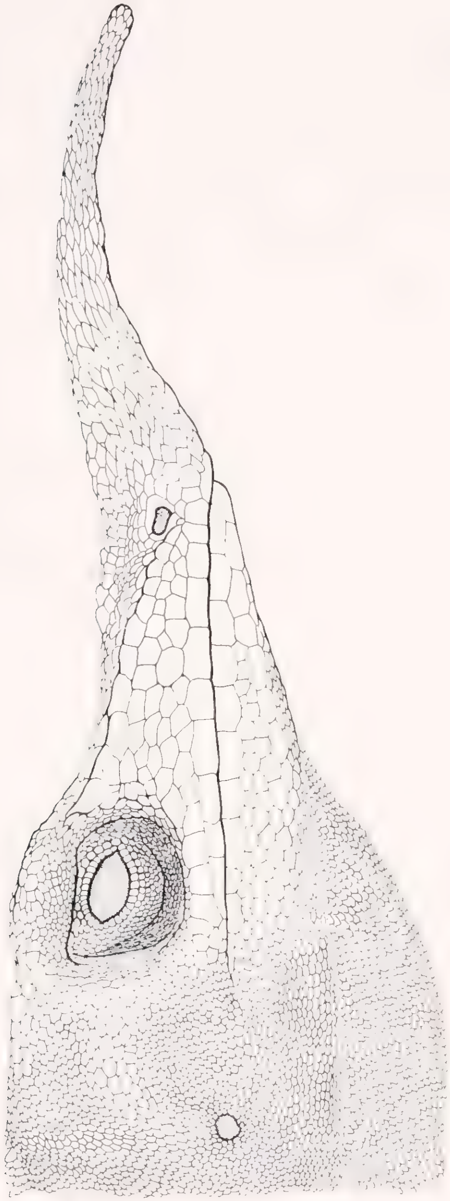

Figure 4. *Anolis proboscis,* USNM 207672. Lateral view of head.

appears to be a soft protuberance which involves the smaller postrostral scales. In *A. phyllorhinus* and *A. proboscis* the rostral remains at the same level of development as in *laevis* but the area above the rostral is expanded into an impressive nose leaf, longest in *A. proboscis.*

The distinction between the *proboscis* and *punctatus* group is thus perhaps somewhat artificial. The morphological sequence is, however, clear and leads from *proboscis* at one extreme back to *punctatus* at the other. I find it convenient to make the distinction at the point at which the scales and tissues above the rostral are involved in the swelling. Since the relation of this area to the rostral is very similar in the three species, it provides greater plausibility for the contention that this is a single lineage. It is not, on the other hand, clear that *A. punctatus* is directly related to the species that mimic it by means of the presence of a projecting rostral in the male. However, any decision on this point is necessarily tentative, and I emphasize convenience rather than certainty of phyletic affinity as a basis for recognition of this group.

Nothing is known of the function of the proboscis (see below) and all nine specimens of this group thus far collected have been males. This has raised (e.g. Peters and Orcés, 1956) the issue that the proboscis anoles might be the males of species already described on the basis of females. However, there are few described species still known only from females. Also the other external characters of each of the proboscis anoles are such that it would require a degree of sexual dimorphism beyond anything known in lizards to make any of the three proboscis species possibly conspecific with any other described anoles. In the case of *A. punctatus* and the other species with projecting rostrals, this and the presence of a dewlap, enlarged postanal scales and sometimes minor differences in color distinguish the males. Scale counts and other aspects of morphology do *not* significantly differ between the sexes.

Only *A. proboscis* is known from series (the type, three newly collected specimens given to the United States National Museum by Orcés, and two in the Orcés collection in Quito). *A. phyllorhinus* is represented by only two specimens, the type and a badly preserved second specimen. *A. laevis* is still known only from the type, which is now in extremely poor condition.

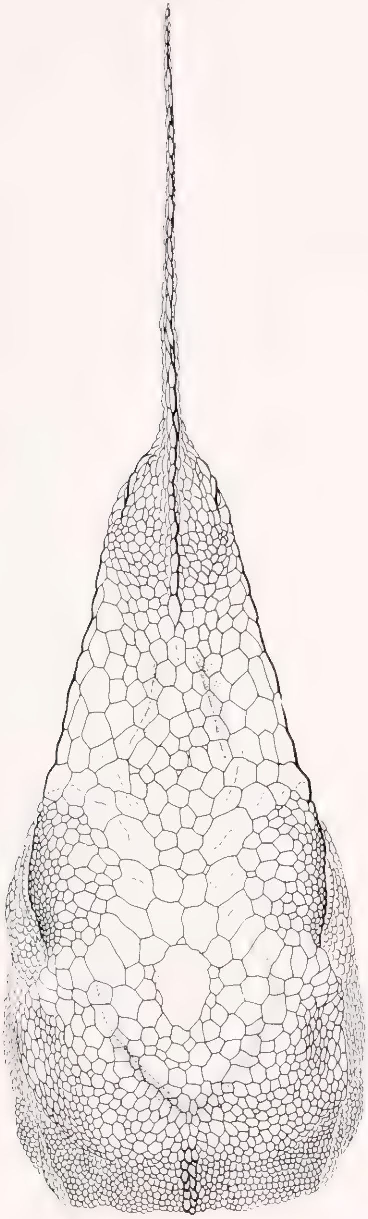

Figure 5. *Anolis proboscis,* USNM 207672. Dorsal view of head.

EVOLUTIONARY ASPECTS

Three species, nine specimens, four localities and one note on habitat are the sum of our objective data on the proboscis anoles. They provide little opening for discussion or for evolutionary speculation.

It is possible, however, to place this minimal amount of data against a background of the much greater knowledge of anoles as a whole. It is a peculiarity of the proboscis anoles that in no other way are they known to be different or indeed especially interesting. The single aspect that appears striking is the proboscis itself.

Other bizarre structures are known in anoles. The dewlap would be bizarre were it less common and less familiar. High tail fins supported by heightened caudal neural spines occur in a number of distantly related species. Casque heads — heads enlarged by crests and ridges — occur in several *Anolis* and in the related anole genera *Phenacosaurus* and *Chamaeleolis*. All these structures — dewlap, tail fin, casque head *and* proboscis – have the effect of increasing the apparent size of the animals that bear them. In the case of the dewlap, there is evidence of use in agonistic encounters, and evidence (Rand 1967) that larger animals usually win in such encounters.

Trivers (1976) has shown the importance of sexual selection for size in one species of *Anolis;* he has inferred the generality of the rule. There are, however, aspects of increase in real size that make the course of evolution complex. A real increase in size with its implied increase in weight can carry with it functional restrictions that compel changes in the life style of the species that exercises this option. Sometimes such changes are realized within the ontogeny of a single species. Sometimes we see them as the alternative strategies utilized by sympatric species (Schoener, 1970; Williams, 1972). Virtual changes in size — unreal but visually effective — are still another alternative. Virtual size has the advantage of introducing few if any functional problems.

I have called attention to elongation of the head in many crown anoles (Williams, 1965). It is probable that this initially has a (still undefined) functional explanation. However, there are side effects: the change of head shape probably has its species-recognition aspects and the size of the head has its agonistic advantage aspects. Yet if these latter aspects have too much effect, the bony structure of

Figure 6. *Anolis proboscis,* USNM 207672. Lateral view.

the head is elongated beyond its functional optimum. There will therefore again be a premium on virtual rather than real change of head shape. We see the beginning of such a phenomenon in *Anolis punctatus* and in some related species where (in males) only the rostral scale is enlarged. *A. laevis* carries this process a slight step further. *A. phyllorhinus* and *A. proboscis* have gone much further.

It is significant that the probosces in *A. phyllorhinus* and *A. proboscis* are not similar in detail. One would expect this if there were functional aspects to the structure *per se.* On the contrary, it appears a similar visual effect may readily be achieved by only broadly comparable means. This corresponds with species recognition devices and intra-species display where there is no requirement that structures be similar; rather the requirement is that they be different. (In view of the wide allopatry of the known proboscis anoles, there could be no selection for striking difference *now,* but perhaps it has existed in the past.)

Within the Iguanidae, the basiliscines would seem to be quite parallel cases. Head casques — very different in structure — are present in all three genera; in *Basiliscus,* dorsal and tail fins are present, different and wonderfully conspicuous in three species, very reduced in a fourth. (Once a bizarre structure has been adopted as an intra- and interspecies signal, an option open to a new member of a group is to abandon the structure: absence of a signal is itself a signal.) The absence of a dewlap is a strategy adopted by two species in the very complex anole fauna of Cuba; the dewlap is consistently retained in the simplest faunas and is reduced only in the fauna almost as locally complex as Cuba, that of Hispaniola (Williams and Rand, 1977).

Outside the Iguanidae, a number of species in the closely related family Agamidae show parallels to the proboscis anoles: *Ceratophora* (Ceylon, three species, see M. Smith, 1935 and Taylor, 1953); *Harpesaurus* (Java, Sumatra, Nias, five species *fide* Wermuth, 1967); *Lyriocephalus* (Ceylon, one species, Taylor, 1953) and *Cophotis* (Ceylon and Sumatra, De Roois, 1915). The probosces in these are all soft structures but considerably more variable in shape, number and squamation than those of the proboscis anoles. (Figs. 7–9 show the differences within the genus *Ceratophora.*) For chameleons Rand (1961) has already discussed the function of the ornamentation that is so remarkably developed in the montane

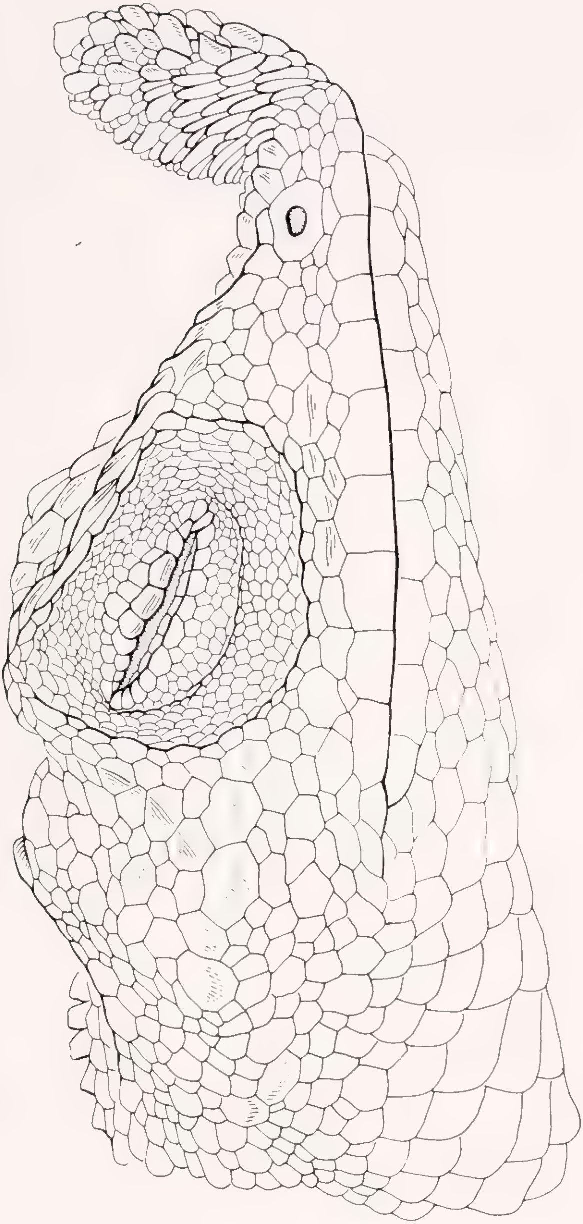

Figure 7. *Ceratophora tennenti,* MCZ 136187. Side view of head.

species of Africa. In the horned chameleons, however, the ornament is a solid structure. In this case, the ornament may serve a physical function in aggression, as the horns do.

Still further afield, Hopson (1975) has discussed the singular crests of hadrosaurian dinosaurs as cranial display structures. His paper (see also Molnar, 1977) also cites the parallels with mammalian horns and has references to the extensive literature.

Of course, alternative explanations are available for structures such as probosces in *Anolis,* e.g. camouflage. However, such other functions, if they exist, do not disprove the display function of *Anolis* probosces or basiliscine crests. The value of a structure for more than one function is a familiar phenomenon and will, not surprisingly, be sustained by natural selection.

ACKNOWLEDGMENTS

The extant world material of proboscis anoles has been made available to me by the late James A. Peters, W. R. Heyer and Ronald Crombie of the National Museum of Natural History, by Gustavo Orcés-V of the Escuela Polytecnica Nacional, Quito, Ecuador, by Edmond V. Malnate of the Academy of Natural Sciences, Philadelphia and by P. E. Vanzolini of the Museum of Zoology of the University of São Paulo. To all of them I am indebted for their help and kindness. I have discussed the function of the probosces with A. S. Rand. Robert Bleiweiss called my attention to the refugium between the Rios Tapajoz and Madeira cited by Haffer. Laszlo Meszoly has provided the illustrations of the proboscis anoles and of their counterparts in the agamid genus Ceratophora. This study has been supported in part by National Science Foundation grant GB 37731X.

LITERATURE CITED

Barbour, T. 1934. The Anoles II. The mainland species from Mexico southward. Bull. Mus. Comp. Zool. **77:** 119–155.

Boulenger, G. A. 1885. Catalogue of the lizards in the British Museum (Natural History), 2nd ed., London, xiii + 492 pp.

Burt, C. E. and M. D. Burt. 1933. A preliminary checklist of the lizards of South America. Trans. Acad. Sci. St. Louis **28:** 1–104.

Cope, E. D. 1876. Report on the reptiles brought by Prof. James Orton from the Middle and Upper Amazon and western Peru. Jour. Acad. Nat. Sci. Phila. (2) **8:** 159–188.

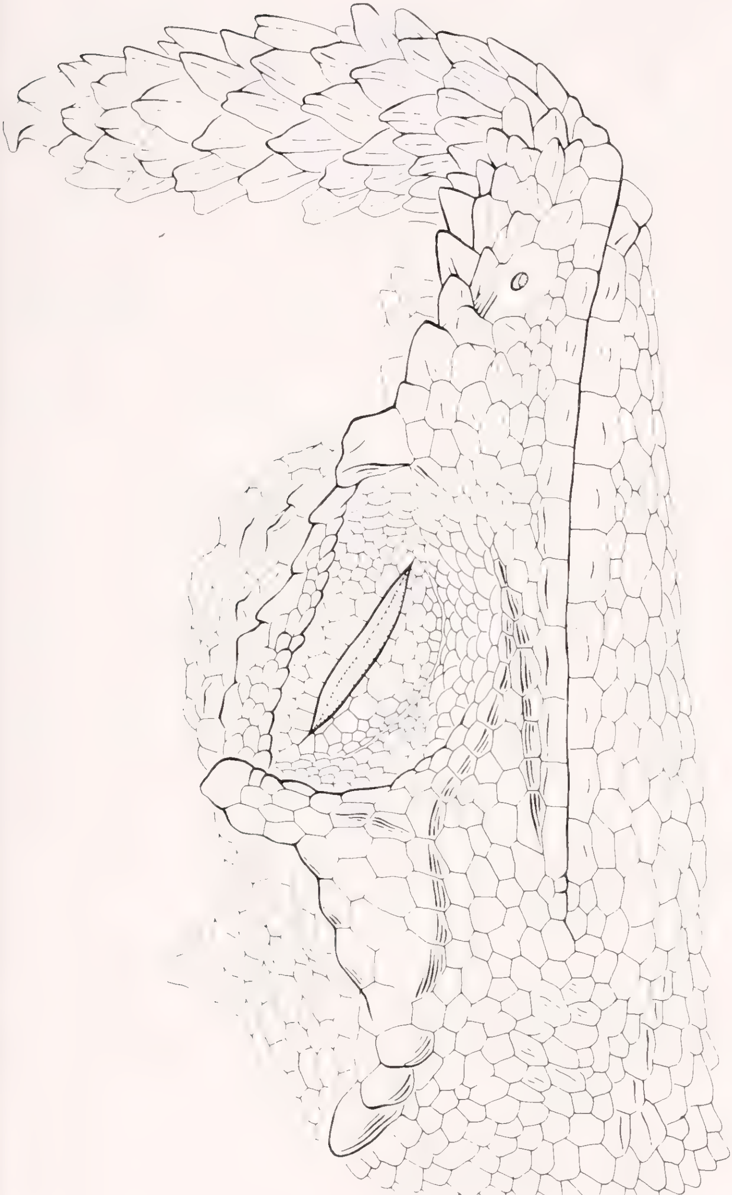

Figure 8. *Ceratophora aspera,* MCZ 4139. Side view of head.

De Rooij, N. 1915. The reptiles of the Indo-Australian Archipelago. I. Lacertilia, Chelonia, Emydosauria. E. J. Brill, Leiden: i-xiv + 384 pp.

Haffer, J. 1974. Avian speciation in tropical South America. Publ. Nuttall Ornith. Club No. 14, Cambridge, England, viii + 389 pp.

Hopson, J. A. 1975. The evolution of cranial display structures in hadrosaurian dinosaurs. Paleobiol. **1:** 21–43.

Malnate, E. V. 1971. A catalog of primary types in the herpetological collections of the Academy of Natural Sciences, Philadelphia (ANSP). Proc. Acad. Nat. Sci. Phila. **123:** 345–375.

Molnar, R. E. 1977. Analogies in the evolution of combat and display structures in ornithopods and ungulates. Evol. Theory **3:** 165–190.

Myers, G. S. and A. Carvalho. 1945. A strange new leaf-nosed lizard of the genus *Anolis* from Amazonia. Bol. Mus. Nac. Rio de Janeiro N.S. **43:** 1–14.

Peters, J. A. 1967. The lizards of Ecuador, a checklist and key. Proc. U. S. Nat. Mus. **119:** 1–49.

Peters, J. A. and R. Donoso-Barros. 1970. Catalogue of the Neotropical Squamata. Part II. Lizards and amphisbaenians. Bull. U. S. Nat. Mus. **297:** viii + 293 pp.

Peters, J. A. and G. Orcés-V. 1956. A third leaf-nosed species of the lizard genus *Anolis* from South America. Breviora No. **62:** 1–8.

Rand, A. S. 1961. A suggested function of the ornamentation of East African chameleons. Copeia 1961: 411–414.

______. 1967. Ecology and social organization in the iguanid lizard, *Anolis lineatopus*. Proc. U. S. Nat. Mus. **122:** 1–79.

Schoener, T. W. 1970. Size patterns in West Indian *Anolis* lizards. II. Correlations with the sizes of particular sympatric species — displacement and convergence. Amer. Natur. **104:** 99–103.

Smith, M. 1935. The Fauna of British India, including Ceylon and Burma Reptilia and Amphibia. II. Sauria. Taylor and Francis, London: i-xiii + 440 pp.

Taylor, E. D. 1953. A review of the lizards of Ceylon. Univ. Kans. Sci. Bull. **35:** 1525–1585.

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evol. **30:** 253–269.

Wermuth, H. 1967. Liste der rezenten Amphibien und Reptilien. Agamidae. Das Tierreich **86:** i-xiv + 127 pp.

Williams, E. E. 1965. South American anoles (Sauria, Iguanidae): two new species of the *punctatus* group. Breviora No. **235:** 1–15.

______. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evol. Biol. **6:** 47–90.

Williams, E. E. and A. S. Rand. 1977. Species recognition, dewlap function, and faunal size. Amer. Zool. **17:** 261–270.

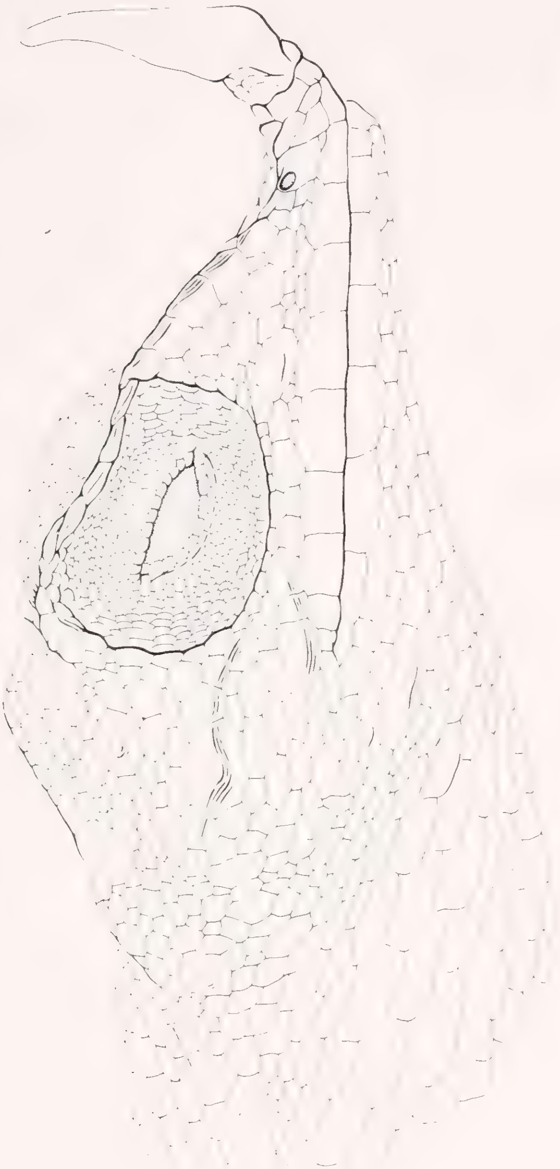

Figure 9. *Ceratophora stoddaerti,* MCZ 116378.